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A CONTRIBUTION TO THE PHYSIOLOGY OF WING DEVELOPMENT IN APHIDS.[1]

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CONTENTS.

I. Introduction.

There are at least two closely related and equally interesting phenomena observed in the aphids, or plant-lice as they are commonly called. These are the development of apterous or alate forms, or both, as the offspring of either a winged or apterous viviparous female, and the parthenogenesis exhibited by them. The phenomena are not the result of alternation of generations, for it has been found by Slingerland (1893) and others that under certain favorable conditions a species of aphid might continue multiplying for a period of several years without producing a single male or winged individual.

Several attempts have been made to explain the phenomenon of wing-development in aphids. Shortage of food supply, it is believed, will usually produce winged aphids so that they may fly away to other plants where the supply of food has not been

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exhausted. Climatic changes, especially the approach of cooler weather, humidity, the wilting of host plants and many other factors have been regarded as possible causes of the appearance of the winged aphid. All explanations, however, have been advanced as the results of observations rather than as the results of experimental work.

The first experimental study of the problem was undertaken by Professor W. T. Clarke, of the University of California, in 1901. He planted a rose twig bearing an apterous parthenogenetic female in each of a series of four-ounce tumblers. These he filled with washed sand, moistened with solutions of several salts or pure water. By this method, he could charge with any desired solution the sap-sucking insect through the plant. He was influenced, so he states, in his choice of chemicals by the chemical analysis of the ingredients of plants. Professor Clarke used sodium hydroxide, sodium phosphate, magnesium sulphate, magnesium chloride, and distilled water as a check. As a result of such experiments, he found that among these substances only the magnesium salts would produce winged aphids. Changes of temperature, he suggested, may not be a factor in the development of the wing in aphids.

In 1908 Professor C. W. Woodworth expressed his views on the problem. He stated that he believed that the wilting of plants might help develop the wing by retarding the growth of other parts and giving an even chance for the wing buds to develop.

Mr. J. D. Neiils, who studied the problem in 1912, not only confirmed the findings of Clarke, but also pointed out a new fact that three days were usually required for the magnesium salts to produce a large number of winged aphids. Further, he found that the young aphids become winged, if they are subjected to the magnesium solutions within three days after birth.

Professor Clarke, and also Mr. Neiils, worked on a single species, namely, the common rose aphid, using the limited series of chemicals above mentioned. In order to determine whether other salts than those of magnesium would have a similar effect on the production of winged aphids, and also to determine whether the results of Clarke and Neiils were applicable to other species of aphids, I undertook an experimental study of the problem.

Before going further, the writer wishes to acknowledge his indebtedness to Professor Woodworth, at whose suggestion the work was begun. His hearty thanks are also due to Professor E. Van Dyke, who, jointly with Professor Woodworth, gave valuable criticism and helpful suggestions during the progress of the investigation.

II. Experiments with the Rose Aphid.

These were partly to verify the findings of Professor Clarke and partly to make a more extensive test of the action of chemicals. The method of experimentation was that adopted and carried out by Professor Clarke. Sharp, clean sand was washed several times in running water, and then left to soak over night. The following day it was washed again with distilled water and after drying was ready for use. Four-ounce tumblers were then filled to one half of their depth with this sand and moistened with solutions of various chemicals. In each of these tumblers, a rose twig bearing from one to three viviparous females, usually apterous, was planted. Though Mr. Neiils pointed out the fact that three days are usually required for the magnesium salts to produce the largest number of winged aphids, it is not always necessary that the mother aphids be transferred to the twig that number of days after it is planted, to see the effect of the salts, for, as is also stated by Mr. Neiils, the young aphids become winged if they are subjected to magnesium salts within three days after birth. Consequently, I used the method previously described. A careful watch was kept of the twigs and when winged forms appeared, they were taken away, and the records kept of their appearance, as well as of the total number of young born. In my later experiments, the record was taken only once, when the first born had acquired the wings, because I had found that the tendency of the young aphids to produce wings could be accurately determined a certain number of days after birth.

I had thought that some other substances might also produce winged aphids. This belief was suddenly strengthened when I found, late in November, that a rose twig that was planted in an old tin can containing ordinary water, was infested with 126

winged and 2 apterous forms. This, I thought, was due to the presence of either tin or iron, because ordinary water, as will be seen elsewhere in the table, never produces more than 5 per cent. of winged forms. Consequently, I tested several salt solutions of the heavier metals and obtained the results which not only confirmed my belief, but also incidentally led to the finding of several new salts which could develop winged aphids.

Sugar and urea were also used in order to determine the effect of electrolytes as well as osmotic pressure. Urea never, or very rarely, produced winged individuals. The action of cane sugar caused rather confusing results, because the young ones produced on twigs, placed in the sugar solution that had been standing for a few days, remained apterous, while those on twigs in fresh sugar solution produced winged forms. These apparantly contradictory results, it was first thought, might be due to the decomposition of sugar by fermentation. That this explanation may be correct is indicated by the fact that both alcohol and acetic acid always produced apterous forms. From December 8th on, the practice was followed of transferring the twig to a fresh solution every three days with uniform results.

When a stronger solution, about *m*/20 of strontium bromide or strontium chloride was used, the tips of the twigs would dry out in the course of from 36 to 48 hours. Many aphids would fall off the twigs; those staying on the twigs would change to a dark salmon color, lose water, and finally dry upon the twig. Even in a solution of *m*/100–*m*/300 of strontium bromide, the twigs planted in it became darker in color and emitted the characteristic odor of strontium salts. About 99 per cent. of the young aphids remaining on the twig developed no wings.

Calcium chloride produced the same, but a weaker effect on the twig and also on the aphids. All aphids stayed on the twig charged with *m*/50 solution of the salt, but remained apterous.

Owing to the very poisonous nature of the chemicals used, often the entire number of the young born on a twig charged with the solutions of mercury, lead or copper salts, would drop off before it could be determined whether they were winged or not. But the fact that some of them, happening to remain long enough, produced wings indicated that the solution had the wing-develop-

TABLE I.

EXPERIMENTS WITH ROSE APHIDS.

Date.	Chemicals.	Total No. of Winged Individuals.	Total No. of Apterous Individuals.
Up to October 20	$CaCl_2$	2	83
	H_2O, distilled	0	62
	H_2O, tap	7	112
	KCl	0	58
	Na_2CO_3	0	38
	NaOH	1	153
	$MgSO_4$	182	4
	Sugar	18	34
	$SrCl_2$	1	40
	Urea	2	32
October 22	$CaCl_2$	0	42
	H_2O, distilled	0	24
	KCl	0	42
	$NaHpO_4$	0	28
	$MgSO_4$	84	1
	$SrCl_2$	0	14
	Sugar	36	25
	Urea	0	24
	$MgSO_4$—NaOH	22	2
	$MgSO_4$—Na_2CO_3	30	5
	$MgSO_4$—Na_2CO_3	2	16
	Acetic acid	0	52
November 11	Ordinary water	2	24
	KCl	0	27
	NaOH	0	52
	$MgSO_4$	142	1
	Mg citrate	28	1
	Sugar	82	0
	$SrCl_2$	1	14
	Tin can	38	3
	NaOH—$MgSO_4$	48	11
December 2	Alcohol	1	48
	$CaCl_2$	0	14
	H_2O	0	48
	KCl	0	20
	NaOH	0	48
	Na_2CO_3	1	143
	$MgSO_4$	12	0
	Mg citrate	24	0
	Tin can H_2O	62	0
	Tannin	0	14
	$SrCl_2$	0	28
	Creek water	3	87
	Urea	0	18
December 18	$SrCl_2$	33	1
	$CuSO_4$	12	0
	$Hg(NO_3)_2$	6	1
	$NiSO_4$	86	0
	$ZnCl_2$	38	1
	$SnCl_4$	92	0
	$AgNO_3$	11	0
January 20, 1913	$Hg(NO_3)_2$		
	$MgSO_4$	8	0
	$NiSO_4$	141	0

Date.	Chemicals.	Total No. of Winged Individuals.	Total No. of Apterous Individuals.
January 20, 1913	$PbCl_2$	2	0
	$SbCl_3$	18	2
	$SnCl_4$	148	4
	Na_2CO_3	0	53
	NaOH	0	38
	Urea	0	14
	Sugar	1	85
	Alcohol	0	62
	Tannin	1	14
	Alum	1	82
	H_2O	0	28
February 7	$CuSO_4$	5	0
	KCl	0	59
	H_2O	0	48
	$NiSO_4$	62	0
	NaOH	0	48
	$SnCl_4$	111	1
	$ZnCl_2$	2	
February 21	$CaCl_2$	0	52
	$CuSO_4$	5	1
	$AgNO_3$	12	0
	$HgCl_2$	17	4
	H_2O	1	148
	KCl	1	14
	$SrCl_2$	0	29
	Na_2CO_3	0	24
	$SnCl_4$	184	1
	$MgSO_4$	17	1
	$PbCl_2$	10	2
	$ZnCl_2$	8	1
	Alcohol	1	42
	Acetic acid	0	14
March 5	$AgNO_3$	2	0
	$CaCl_2$	0	33
	KCl	2	54
	H_2O, surface	2	142
	H_2O, distilled	0	22
	$HgCl_2$	8	1
	$MgSO_4$	31	1
	$NiSO_4$	110	2
	Na_2CO_3	0	87
	$SrCl_2$	0	42
	Sugar	1	15
	Urea	2	18
March 20	$AgNO_3$	14	0
	$CaCl_2$	0	48
	H_2O, distilled	6	114
	KCl	0	61
	$SrCl_2$	0	32
	$MgSO_4$	36	1
	Mg citrate	44	0
	Na_2CO_3	1	20
	$NiCl_2$	98	1
	$SnCl_4$	112	3
	Urea	1	16
	Sugar	218	1

Date.	Chemicals.	Total No. of Winged Individuals.	Total No. of Apterous Individuals.
April 3	$AgNO_3$	12	0
	Alcohol	0	136
	$CaCl_2$	6	62
	$CuSO_4$	12	0
	KCl	0	47
	H_2O, tap	2	48
	$MgSO_4$	32	0
	$NiSO_4$	182	1
	NaOH	0	84
	$NaCO_3$	0	92
	$SrCl_2$	0	24
	$SnCl_4$	116	0
	Sugar	118	1
	Urea	0	31
	Alum	0	16
	Peptone	1	15
	Sugar + $MgSO_4$	0	24
	Sugar + Na_2CO_3	1	82
	$MgSO_4$ + NaOH	0	62
	Sugar + NaOH	0	40
	Sugar + NaOH	0	12
	Sugar + NaOH	2	12
	Sugar + NaOH	0	42

The following is the summary of the foregoing data.

	Winged Individuals.	Apterous Individuals.
$AgNO_3$	51	0
$CuSO_4$	34	1
$HgCl_2$	31	6
$NiSO_4$	955	5
$SbCl_3$	41	5
$PbCl_2$	12	2
$SnCl_4$	579	8
$ZnCl_2$	49	2
Mg salts	840	9
Sugar	512	4
Alcohol	288	2
Alum	3	34
Acetic acid	0	67
Na salts	2	1029
Ca salts	1	433
K salts	3	324
Sr salts	1	220
Tannin	1	14
Urea	5	153
Water, distilled	0	394
Water, tap and creek	17	461
Peptone		15

ing qualities. Only a few drops of the normal solutions of these salts were added to the 5 c. c. of distilled water, in most of my experiments.

The above results not only verified the findings of Professor Clarke, but also led to the discovery of new substances. In addition to the magnesium salts, salts of antimony, nickle, tin, mercury, lead, zinc and also sugar were found to produce winged aphids; while alcohol, acetic acid, alum, tannin, salts of strontium, potassium and calcium, and also urea were shown to have no effect. These substances may, therefore, be classified into wing-developing and non wing-developing substances, respectively, according to their action on the wing buds. To the former class, belong the salts of alkalis and the alkaline earths, while to the latter belong all of the other salts mentioned, as well as sugar.

III. Experiments with Other Species of Aphids.

The studies thus far mentioned concerned only the common rose aphis. Do these substances have a similar effect upon other species of aphids? I, therefore, instituted another series of experiments, using the same methods as were employed in the course of the development in the rose aphid.

The following results were obtained (Table II.):

As is shown in this table, the results obtained with these aphids are not different from those obtained with the rose aphids, *i. e.*, alkali salts and salts of alkaline earth, together with distilled water, tannin, alcohol and acetic acid produced no winged aphids, while the rest of the salts and also sugar produced winged forms in these species, as they did in the rose aphids.

The periwinkle aphids, as will be noticed in the table, never yielded one hundred per cent. of winged individuals with ordinary strengths of wing-producing substances; *e. g.*, a fifteen per cent. solution of sugar or $m/40$ of magnesium sulphate. Subjection to a very weak solution of the alkali salts, or even to distilled water, did, on the other hand, completely suppress the development of the wings. Thus, although the number of the winged forms produced on twigs charged with wing-producing substances was small, their appearance must be accredited to the presence of these substances. The common aphids on Sonchus, on the mustard and on the German ivy (*Senecio* sp.) were found to develop their wings after subjection to very weak solutions of

TABLE II.

Date.	Substances.	Species of Aphids.							
		Mustard Aphid.		Sonchus Aphid.		Periwinkle Aphid.		Senecio Aphid.	
		No. of Winged Forms.	No. of Apterous Forms.	No. of Winged Forms.	No. of Apterous Forms.	No. of Winged Forms.	No. of Apterous Forms.	No. of Winged Forms.	No. of Apterous Forms.
Up to Oct. 20	H_2O	228	2						
	KOH	2	48						
	$MgSO_4$	145	2						
	Sugar	24	2						
	H_2O	2	62						
	$MgSO_4$	12	0						
	Sugar	51	0						
Nov. 11	H_2O, tap			1	27				
	KCl			0	16				
	$MgSO_4$			37	0				
	Sugar			72	0				
Nov. 25	$MgSO_4$	82	1	40	0	8	10		
	Sugar	28	0	27	27	7	12		
	H_2O			0	12	0	42		
Dec. 4	H_2O	2	24	1	28	0	28		
	$MgSO_4$	25	1			8	6		
	Sugar	78	0	42	0	12	10		
	Tin can and tap water					10	30		
Feb. 27	H_2O	4		4	41	0	12	4	41
	$NiSP_4$			15	0	2	8		
	$MgSO_4$			12	0	8	11		
	$SnCl_4$			20	2	14	6		
	KCl			0	14	0	10		
	$CaCl_2$			0	32	1	18		
March 14	$CaCl_2$							1	12
	$MgSO_4$							20	0
	$SnCl_4$							112	2
	H_2O							0	81
March 27	H_2O			0	28	0	72	2	142
	KCl					0	72	0	129
	Na_2CO_3					6	10	0	60
	$CaCl_2$							1	28
	Sugar							12	0
	Urea							0	6
	$MgSO_4$					12	45	28	1

any of the wing-producing substances. Thus, it is evident that there exists a variation in the degree of susceptibility among the species of aphids.

It might also be well to add here that in several species of aphids belonging to the tribe Chaitophorini no apterous viviparous females have as yet been found. Such, for example, is the

case with the chestnut aphis (*Myzocalis castanæ*), the ulmus aphis (*M. ulmi*), the oak aphis (*M. quercus*, etc.), the birch aphis (*Euceraphis betulæ*), the linden aphis (*Eucallipterous tiliæ*) and others. These species do not grow on any other host plant except their specific ones, nor are they easily reared on cuttings, or even on young potted seedlings. Although the writer failed to produce apterous forms of these Chaitophorini, the development of wings in these species is no doubt due to the nature of the host and also due to the feeding habits of the aphids, for all the young are apterous.

The aphids infesting willows, wheat, clematis, pea, radish and other plants were occasionally experimented with, several substances being used, as in other experiments. The development of the wings in these aphids could also be controlled.

IV. The Period during which the Development of the Wings may be Controlled.

Professor Clarke has suggested that the fate of the wing-buds may probably be determined near the end of the first molt, while Professor Woodworth thinks it can be predicted as early as one day after birth. The fact that one hundred per cent. of winged aphids can be produced on a twig charged with magnesium salts as late as three days after planting the twig, led Neiils to carry on a series of experiments along this line. By transplanting young aphids from a twig charged with distilled water to one charged with magnesium salts, he found that rose aphids could be made to produce wings if they were subjected to the magnesium solution within three days after birth. I have partly repeated his experiments and also extended them to other species with the following results:

It is seen from the above results that the period during which the development of the wing-buds can be controlled varies with the species. I have also observed in the course of my experiments that the aphids infesting the German ivy (*Senecio* sp.) develop the wing-buds within sixty hours after their birth.

TABLE III.

Date.	Name of Plant.	Total No. of Young Transferred.	Sol. on which Young were Born.	No. of Days left on H_2O.	Sol. to which they were Transferred.	No. that Remained Wingless.	No. that Developed Wings.	Per Cent. of Winged Forms.
Oct. 8–18,	Rose	10	H_2O	1	$MgSO_4$	1	9	90
1912	"	10	"	2	"	0	10	100
	"	10	"	3	"	0	10	100
	"	10	"	4	"	2	8	80
	"	10	"	5	"	9	1	10
	"	10	"	6	"	9	1	10
Nov. 30–	"	10	"	1	"	1	9	90
Dec. 9	"	10	"	2	"	0	10	100
	"	10	"	3	"	0	10	100
	"	10	"	4	"	3	7	70
	"	10	"	5	"	8	2	20
	"	10	"	6	"	9	1	10
	Sonchus	10	"	1	"	0	10	100
	"	10	"	2	"	0	10	100
	"	10	"	3	"	0	10	100
	"	10	"	4	"	0	10	100
	"	10	"	5	"	0	10	100
	"	10	"	6	"	3	7	70
Feb. 10, 1913	Rose	10	"	1	"	0	10	100
	"	10	"	2	"	0	10	100
	"	10	"	3	"	1	9	90
	"	10	"	4	"	0	10	100
	"	10	"	5	"	2	8	80
	"	10	"	6	"	10	0	0
	"	10	"	8	"	9	1	10
	Sonchus	5	"	1	"			
	"	5	"	2	"			
	"	5	"	3	"			
	"	5	"	4	"	0	10	100
	"	5	"	5	"	0	10	100
	"	5	"	6	"	0	10	100
	"	5	"	8	"		2	20
	"	5	"	9	"		0	0
	Mustard	5	"	1	"			
	"	5	"	2	"			
	"	5	"	3	"			
	"	5	"	4	"		10	100
	"	5	"	5	"		10	100
	"	5	"	6	"		10	100
	"	5	"	8	"		8	80
	"	5	"	9	"		0	0

V. STRENGTH OF MAGNESIUM SULPHATE NEEDED TO PRODUCE THE WINGED APHIDS.

It must be conceded that no accurate methods of measuring the amount of any solution can be devised, for the reason that the solution must first pass through the plant tissue before it reaches the body of the insect. For the purpose of obtaining

some idea of the amount of the wing-developing substances to be effective in the development of the wing-buds, I instituted a series of experiments. In these experiments, the solutions of the magnesium sulphate, of various strengths, were poured directly into a series of tumblers, in each of which a rose twig, bearing a viviparous female, had been placed.

TABLE IV.

Date.	Solutions.	No. Winged.	No. Apterous.	Per Cent. Winged.
Oct. 9.....	*m*/2	8	2	80
	m/3	3	0	100
	m/4	5	0	100
	m/10	13	0	100
	m/20	33	0	100
	m/100	16	1	92
	m/200	112	4	95
Dec. 12...	*m*/20	6	1	86
	m/20	5	0	100
	m/80	18	1	90
	m/320	38	1	97
	m/50	10	0	100
	m/100	22	1	95
Feb. 25 ...	*m*/100	52	0	100
	m/200	52	0	100
	m/400 ?	12	2	90
	m/500 ?	212	4	98
	m/1000 ?	113	6	96

As will be seen from the table, I have been unable as yet to reach the lowest strength at which the majority of the aphids born on the twig would remain apterous. The table, however, suggests that this minimum amount may lie beyond the strength of an *m*/1000 solution.

It may also be added here that the susceptibility to the chemicals varies greatly with the species. *Euceraphis betulæ* on the birch tree growing on a sunny soil rarely or never produces apterous forms, while a considerable number of *Calaphis betulacolens* infesting the same host become winged. *Macrosiphum rosæ* also produce alate forms even on a relatively younger shoot, but it is utterly impossible to raise winged *Myzus persicæ* on a similar host without the application of a wing-developing substance.

VI. On the Physical Factors.

1. *Temperature.*—No special experiment for determining the effect of temperature upon the development of the wings has

been made. A part of my experiments, and also those of Professor Clarke, were carried on in our laboratory where a nearly uniform temperature was kept throughout a period of several days. A larger part of my work was done in an old greenhouse where the change of temperature between day and night was exceedingly great. I have also done a part of my work out of doors. In all of these cases, only a very few of the winged aphids appeared on the twigs charged with any of the non-wing-developing substances. Professor Clarke stated that he had subjected aphid-infested twigs charged with distilled water to a sudden change of temperature from 80° F. to 30° F., and had observed no effect on the wing development. These observations, therefore, establish the fact, I believe, that changes in temperature have no effect on the production of winged forms.

The popular conception that the approach of cold weather makes winged aphids appear may be explained in the following manner. Plants mature either at the time when the cold weather sets in or previous to that period. They also manufacture, through the agency of their leaves and under the influence of sunlight, starch, which at this maturing period is changed to sugar and stored away in other parts of the plant. This sugar is the most common wing-developing substance, as we have seen. Therefore, the aphids produce wings at the approach of cold weather, not because of the low temperature, but because of the presence of sugar in the plant tissues at that time.

2. *Wilting of the Plant.*—Professor Woodworth has pointed out that when the plants, especially cabbages on which he has made extensive observations, are badly infested with aphids and begin to wilt, there was a decrease in the birth rate of the insects and a "spontaneous appearance of the aphids with wing-pads was noticed." His explanation of this phenomenon is that the wilting of plants probably causes an effect similar to that produced by the magnesium salts, that is, it makes it possible for the wing-buds to have an even chance with the rest of the body to develop. Under more favorable conditions, he suggests that the growth of the wing-fundaments might be retarded on account of the faster growth of the other parts of the body. A morphological study bearing upon this point is pre-

sented farther on, but I shall now attack the problem by experimental means.

The weight of a number of fresh rose twigs, similar to those used in my other experiments, was recorded. One of these twigs was then planted in a tumbler containing distilled water, and one in a tumbler containing calcium chloride, in the manner already described. Three days later, the twigs were taken out of the tumblers, placed on a paper, and left to dry from four to twenty-four hours. The second or dried weight of each was recorded, and the twigs then replaced in their respective tumblers. Three to four apterous viviparous females were then transferred to each of them, and a careful watch kept for the young. The following tabulation shows the results obtained:

Table V.

The Effects from the Wilting of the Plant.

Date.	Chemicals.	Series.	Wt. of Fresh Plant.	Wt. of Dried Plant.	Per Cent. of Water Lost by Evaporation.	No. of Winged Aphids.	No. of Wingless Aphids.
Dec. 1...	H_2O	1	1.00 gr.	.90 gr.	10	1	24
	"	2	1.60 "	1.00 "	38	0	18
	"	3	1.60 "	1.40 "	12	0	4
	"	4	1.80 "	1.00 "	44	0	8
	"	5	2.00 "	1.50 "	25	0	12
	$CaCl_2$	6	1.60 "	.95 "	40	0	4
	"	7	.90 "	.50 "	44	0	16
	"	8	1.10 "	.65 "	40	0	6
	"	9	1.00 "	.50 "	50	0	4
	"	10	1.10 "	.60 "	45	0	8
Mch. 28..	H_2O	1	14.5 "	12.5 "	14	0	38
	"	2	1.60 "	.96 "	40	0	4
	$CaCl_2$	3	1.15 "	.60 "	49	1	8
	"	4	1.40 "	.90 "	36	0	4

Thus the mere wilting of the plant is not a factor in the production of the winged aphids. The drying out of the plant may, however, indirectly help to produce the winged insects by concentrating the ingredients in the plant tissues.

VII. Morphological Study.

The young female aphids are, externally at least, well developed at the time of their birth. They have three pairs of legs and a pair of antennæ as stout as their mother's, but shorter. A pair of so-called honey-tubes and the caudal appendage are also

present. There is, however, no external indication of the wings or of their buds. The body is almost columnar, with a constriction back of the head, but with no marked differentiation between the thorax and abdomen.

In those individuals which ultimately become winged, the second and the third thoracic segments begin to swell laterally as well as dorso-ventrally. The swollen thorax is ordinarily noticeable at the end of the first ecdysis in the case of the rose aphids. Usually after the second, yet occasionally after the third ecdysis, in the case of the mustard aphis, a pair of hyaline wing-pads protrude from each side of the second and third thoracic segments. At the following ecdysis, the wing-pads become unfolded and the adult insect results. In those forms which remain apterous, no constriction between the thorax and abdomen occurs.

Other structural differences noticeable between the apterous and alate viviparous females of the common rose aphid, *Macrosiphum rosæ* (L.), may be tabulated as follows:

Winged Viviparous Female.	Wingless Viviparous Female.
Color—Dorsal marking present.	Dorsal marking absent.
Length—2.2 mm.	2.7 mm.
Antennæ—Articles I to VI dark throughout.	Only I, II, and VI dusky.
Sensoria on III—More than 60 found throughout the entire length.	About 12, all being found near the basal portion.
Color of Cornicle—Dark throughout.	Dark with lighter rings near the base and apex.

These are some of the more prominent differences. Minor differences, as, for example, the relative length, shape, size, etc., of the cornicle, cauda, antenna, etc., are numerous and cannot be enumerated here. It follows, then, that the factor which is responsible for the production of either the apterous or the alate forms not only determines the fate of the wings, but also causes other morphological changes as above mentioned.

Although no special effort was made to study the histological differences between the two forms, the sectioned material showed that there is a less amount of muscles and ectodermal cells, but more of fat body in the apterous form as compared with the alate individual.

VIII. General Discussion.

As the result of our experiments, we have been able to distinguish two groups of substances, one that produces and the other that does not produce winged aphids. *Clarke* (1901), *Neiils* (1912) and *Woodworth* (1908) held that the presence of magnesium in the plant tissue might be responsible for the phenomenon under discussion. My experiments have shown that the magnesium salts are not the sole substances that produce the winged aphids. Other substances, namely, the salts of heavy metals, had a similar effect on the development of wings. Consequently, it becomes clear that what is really responsible for the appearance of the winged aphids is the excess of magnesium and other wing-producing substances over the non-wing-producing substances contained in the plant sap.

Morgan (1909) presented an analysis of the leaves of plants, the rose and the maple, at two different seasons of the year, namely, June and October. His table showed, as we should expect, a marked difference in the amount of ash contained in the leaves of the two kinds of plants at the same time of the year. A similar difference was also pointed out in the case of the same plant at two different seasons of the year. The chemical analysis of plants is, then, in accordance with the general observation in the field that the alate forms are more abundant during the autumn than in the spring and that the winged forms of the same species are more abundant on one kind of plant than on another even at the same period of the year.

Morgan's table is also valuable in estimating the proximate amount of wing-developing substances that may be effective. According to the analysis, the percentages of ash contained in the fresh rose leaves in October and June are 3.61 and 3.69, respectively. The difference between these two figures, or 0.541 per cent., may then be regarded as the maximum amount of the wing-developing substances which would be effective when added to the spring leaves.

I have already given an explanation of why the drying of plants produced alate forms as reported by Woodworth (1908). However, I did not discuss the secondary effect of temperature on the development of the wing. Recently Ewing (1916) stated

that a great number of alate forms would appear under a certain optimum temperature in the form he had been experimenting with, namely, *Aphis avenæ.* I have already shown that the temperature had nothing to do with causing the appearance of the winged forms under a well-controlled environment. Ewing's result, like that of Woodworth on the effect of dryness, was obtained under natural conditions, with perhaps little attention paid to the chemical constituents of the host plant. It is strongly doubted whether any winged forms would have appeared, had they been reared under his optimum temperature but on the host charged with any one of the non-wing-developing substances. In fact, I believe that the appearance of winged forms under his "optimum temperature" is due, not so much to the direct action of heat as such, but indirectly to either an increase in the solubility of the wing-developing substances or to a decrease of the non-wing-developing substances.

Tannreuther (1907), who has made extensive observations on the life history as well as the genetic cycle of *Pterocomma salicis* and *P. salicicola*, says: "The prevalent idea that the development of aphis is unstable and controlled directly by external conditions is certainly very misleading especially in the idea that unfavorable conditions or lack of food is a direct cause for the appearance of the winged and sexual forms. We find in the species studied that just the reverse is true, and that the greatest number of winged forms are found in the second parthenogenetic generation; here in some instances ninety-five per cent. may become winged, especially those found on the rose in good condition which furnished an abundance of food." *Pterocomma bicolor* and *P. rufurum* found in the vicinity of the University of California campus, however, reacted to the chemicals, but they were peculiar in that they did not produce sexual forms at the sixth generation.

Now I come to the consideration of the question which was set forth by Tannreuther (1907), to wit, "Why some of the hypodermic cells of the thorax begin to divide, emarginate and form the adult wings in a few days." According to Anderson (1893) and others there are two groups of salts, one that excites the muscles and one that has little effect upon them. Our so-called

wing-developing substances correspond with the former, and the non-wing-developing substances to the latter. Further, so far as these non-wing-developing substances are concerned, Herbst (1906), Loeb (1907), and others have proven them to be injurious to other classes of animals. For example, Herbst (1906) found that the addition of potassium salts to sea water suppressed the development of the arms of the *Echinus* larvæ. These investigators have also found that the development of the alimentary canal of the *Echinus* larva was impossible in magnesium-free sea water. Again, Fischer (1903) and others have proven that magnesium salts counteract the effect of saline purgative. All these results obtained with other animals by various investigators suggest that wing-developing and non-wing-developing substances exert, respectively, characteristic action on the organic matter. We have at least two evidences that tend to show that in all probability the two phenomena of the appearance of the winged or wingless individuals may be due to the physiological actions osmosis and surface tension. One of these is the presence of more of the fat cells, which are derived from mesoderm cells, in the apterous forms than in the alate forms, and the other is the fact that the cells of the apterous forms are slightly larger than those of the alate forms. The first of these evidences suggests the probable degeneration of muscle and probably nerve cells at the time when the wing cells are in the process of differentiation. The degeneration may, it must be said, be due to the increase in the cytoplasmic area of the cell and the subsequent loss of the coördination between the nucleus and its surrounding cytoplasm, as is manifested in the case of the fat body. The difference in the size of the two forms may not only strengthen the view just presented, but also explains why the winged forms resemble the male, and the apterous, the sexual females; for the two winged forms, the male and the alate viviparous females are much more highly developed than the two wingless sisters, and are produced by the same factor—the decrease in surface tension and osmosis. These physiological factors osmosis and surface tension produce the male if they act on the egg at the time of polar-body formation, and the winged viviparous female if they act on the larva within three days after birth.

In concluding this paper, it may be added here that in the year 1909 von Baehr made the following prediction: "Meine Beobachtungen an *Schizoneura lanigera* führen mich zu dem Schluss, dass der Factor, welcher bei den Embryonen die zu Geschlechtstieren werden, den Impuls zur Ausbildung der Winterovarien und zur Degeneration der schon ziemlich entwickelten parthenogenetische Eiröhren gibt, wahrscheinlich im kausalen Zusummenhang mit der Entwicklung der Flügel, Brustmuskalatur, Sinnesorgane u. s. w. des Muttertieres steht in dem sie sich entwickeln. Derselbe Factor dürfte wohl die Veranlassung sein, dass einige Eier sich zu Männchen entwickeln, wie es im speziellen Teil ausgeführt wurde, werden nämlich fast immer ausser geschlechtlichen Weibchen noch 1–4 Männchen von derselben Mutter geboren."

IX. Aphis Species Mentioned.

Only the common or vernacular names have been given so far in this paper. It, however, seems necessary to add the scientific names of the aphids I have made use of for the reason that the species of aphids infesting the same host frequently vary with the locality as well as with the season of the year. A list of the specific names, together with some of the more common synonyms, is given below:

1. The small birch aphis:
   Caraphis butulaecolens Fitch.
   Siphonocallis butulecolens Fitch.
2. The clematis aphis:
   Myzus persicæ Sulz.
   Aphis persicæ.
     A. dianthi.
     Rhopalosiphum dianthi.
     Siphonophora achyrantes.
     Myzus malvæ.
     Rhonpalosiphum persicæ Sulz.
3. The German ivy aphids:
   Aphis senecio Swaine (MS.).
4. The California maple aphids:
   Thomasia californica Shinji.

5. The mustard aphis:
   Aphis brassicæ Linn.
6. The Periwinkle aphis:
   Myzus circumflexivum.
7. The green pea aphis:
   Macrosiphum ulmariæ (Schv.).
      Aphis ulmariæ Schr.
      A. pisi Kalt.
      Siphonophora pisi Koch.
      S. ulmariæ Kalt.
      Nectraophora pisi Oestl.
      N. destructor Johns.
8. The large rose aphis:
   Macrosiphum rosæ Beaum.
      Aphis rosæ Linn.
      A. dipsaci Schr.
      Siphonophora rosæ Beaum.
      Nectarophora rosæ Linn.
9. The large sonchus aphis:
   Macrosiphum solanifoliæ.
10. The small sonchus aphis:
   Aphis gossipii Glov.
   Aphis citrulli Ashm.
   A. cucumeris Forbes.

X. Summary.

Results of the observations and experiments reported above may briefly be summarized as follows:

1. Either an apterous or an alate parthenogenetic female may bear young larvæ, some of which may finally attain the winged condition, while the others may remain wingless throughout life.

2. When newly born aphids were reared on rose twigs planted in tumblers, containing washed and sterilized sand which had previously been saturated with the solution of a certain substance, nearly one hundred per cent. of winged individuals appeared on the twigs, while either none or few winged forms developed on the twigs charged with any one of another set of chemi-

cals. For the sake of making a distinction between these two groups of substances, we may call the former the "wing-developing" substances, and the latter, the "non-wing-developing" substances.

3. As far as the tests go, the salts of the alkalis (Na, Cl, K, etc.) and alkaline earths (Ca, Br) with the exception of magnesium, distilled water, urea, alum and others were shown to belong to the non-wing-developing substances, while the salts of the heavy metals, and of magnesium, sugar, and perhaps some others belong to the category of wing-developing substances.

4. The wing-developing substances were only effective when applied within a certain period after birth. This period varied with temperature and also with the species, *e. g.*, the maximum time for the rose aphis, *Macrosiphum rosæ* L., during the early summer was found to be from 2 to 3 days, while under the same conditions from 5 to 7 days was the maximum in the case of the sonchus aphids, *Macrosiphum solanifoliæ* Ashm., the mustard aphis, *Aphis brassicæ* L., etc.

5. The amount of magnesium salts and also of other wing-developing substances needed to produce winged aphids was very small. Subjection to a *m*/100 solution of magnesium sulphate for 12–24 hours produced nearly one hundred per cent. of winged aphids, so far as *Macrosiphum rosæ* was concerned.

6. When twigs planted in the sand saturated with distilled water and calcium chloride were subjected to a drying process, the young aphids born on these twigs remained apterous, whereas on those that had been charged with solutions of magnesium salts or some other wing-developing substances, the greatest number of the winged aphids appeared.

7. When newly born aphids are subjected to a mixed solution of wing-developing and non-wing-developing substances, winged aphids may or may not appear, according to whether or not the solution contains an excess of the wing-developing over the non-wing-developing substances.

8. Variation in temperature, or a sudden change from as high as 100° F. to as low as 35° F., failed to produce winged aphids on the twigs charged with non-wing-developing substances.

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